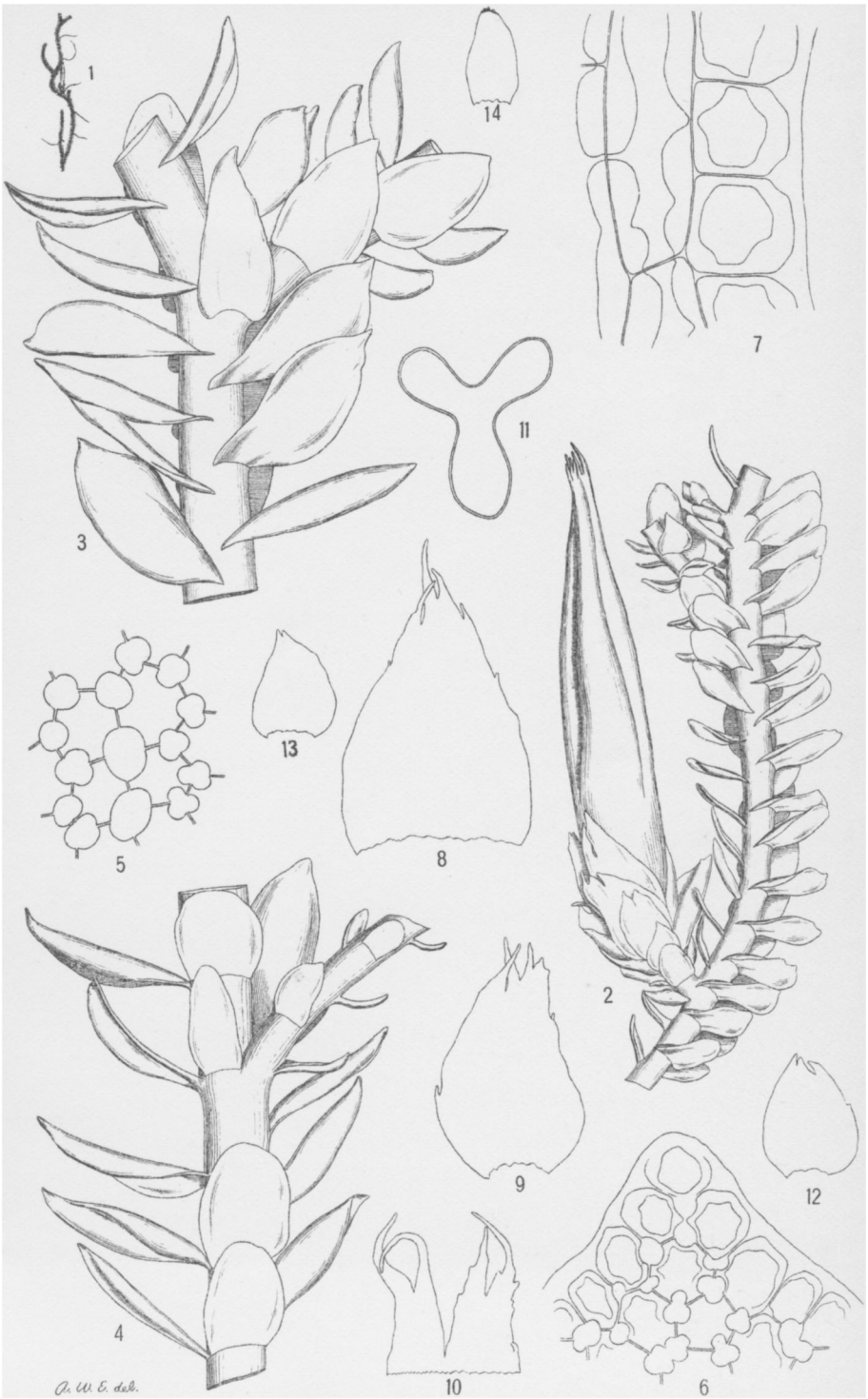
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A new Genus of Hepaticae from the Hawaiian Islands

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(WITH PLATE 1)

Among the tufts of *Herberta sanguinea* collected more than twenty years ago by D. D. Baldwin on the island of Maui, the late C. F. Austin found a few sterile and fragmentary specimens of an hepatic which he recognized as new and doubtfully referred to the genus *Mastigobryum*, as *M. integrifolium*. At my request, Mr. W. H. Pearson kindly sent me, for examination, a portion of Austin's original material. In the packet there is a single stem of the new species, but it is sufficient to show that, although the plant has much in common with *Mastigobryum* or *Bazzania*, as it is now called, it can hardly be retained in this genus, but should rather form the type of a new genus of Hepaticae. The branching of the leafy liverworts was just beginning to receive attention from descriptive hepaticologists at the time Austin wrote, and, as the most essential difference between the new genus and *Bazzania* is a difference in branching, the disposition which he made of his plant was perhaps justified.

An examination of Baldwin's material of *Herberta sanguinea* in the Eaton Herbarium brought to light several additional specimens of this curious species and among them a few showing the floral parts but no perianths. During the past summer, however, Mr. C. M. Cooke, Jr., had the good fortune to find a considerable quantity of the plant on Konahuanui, a mountain about three thousand feet high, on the island of Oahu. As in Baldwin's material, the specimens do not form pure tufts but grow scattered among other hepatics, here, for the most part,

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species of *Bazzania*, *Pleurozia* and *Anastrophyllum*. Both male and female flowers occur somewhat abundantly and a few of the latter show well developed perianths. Mature capsules, unfortunately, are not present. The descriptions in the present paper are drawn almost entirely from Mr. Cooke's material, which has also served for the drawings.

At a cursory glance, the plant looks unlike a typical *Bazzania*; in the first place because its leaves are transversely inserted and strongly squarrose instead of being incubous and appressed, and in the second place, because its underleaves are relatively larger than those of *Bazzania* and are also strongly squarrose. These peculiarities might seem to indicate an affinity with certain genera of the Ptilidioideae, such as *Mastigophora* or *Herberta* or the curious and imperfectly understood *Herpocladium* of Mitten. The position of the sexual organs, however, both male and female, on short branches axillary to the underleaves, shows at once that the true affinities of the new genus are with the Trigonantheae. The bracts and bracteoles, moreover, as well as the fully developed perianths, are essentially like those of *Bazzania* and of certain other genera of this same tribe.

More important as a generic character than the foliar differences just indicated is a peculiar kind of branching, unlike anything hitherto described for the Hepaticae. In the related *Bazzania*, as is well known from the studies of Leitgeb, the branching is of two kinds. In the first, the so-called "Endverzweigung" or "terminal branching,"* the branches are exogenous in origin and lateral, each branch representing the postical half of one of the lateral segments of the apical cell.† The leaf, which normally develops from the whole of such a segment, is here restricted to the antical half and is therefore narrower than an ordinary leaf and not toothed at the apex. A branch here, which is always an ordinary leafy branch, is of about the same size as the axis from which it springs; and, as the axis is itself deflected in the opposite direction from that taken by the branch, the plants of many species appear

* Untersuch. über die Lebermoose, 2 : 22, 23. *pl. 4. f. 2, 4.* 1875.

† Branching from the postical half of a lateral segment occurs in many genera of the Jungermanniaceæ and (with the modification seen in *Radula*, etc.) is the only type of terminal branching described by Leitgeb.

as if they were repeatedly dichotomous. In the second or "intercalary branching,"* the branches are endogenous in origin and postical, arising in the axils of the underleaves. They develop at some distance from the apex, starting just inside the cortical cells of the axis and forcing these apart as they elongate. Around the base of such a branch, it is possible for a long time to find the remains of these ruptured cells in the form of an indistinct sheath. In *Bazzania*, these intercalary branches are always specialized, sometimes as the very short sexual branches but more commonly as the long and slender root-like flagella with their rudimentary leaves. Both of the kinds of branching just described for *Bazzania* occur in the new genus as well, the ordinary vegetative branches (Fig. 3) and the sexual branches (Fig. 2) arising in precisely the same way in the two genera. In rare cases, nevertheless, the Hawaiian plant will show an ordinary leafy branch springing from the axil of an underleaf and therefore intercalary in nature like the vegetative branches of *Kantia* and of the typical species of *Cephalozia*.

The peculiar branches of the new genus are the flagella. These are similar in appearance to those of *Bazzania*, except that they bear small but distinct leaves near the base; but their place of origin is very different. Instead of developing in the axils of the underleaves, each flagellum arises at one side of an underleaf (Fig. 4); instead of being surrounded by an indistinct sheath, showing that it is endogenous in origin, it is naked at the base and is, therefore, exogenous in origin; the underleaf, finally, beside which a flagellum is situated, is much narrower than an ordinary underleaf. All of these conditions point to the fact that we have to do here with a terminal branching in one of the postical segments of the apical cell. This is made even more evident by a study of the apical region, and in this connection it is instructive to compare what we find in this plant with what is found in the apical region of the closely related *Bazzania*.

The early stages of the leaves and underleaves of *Bazzania trilobata* have been carefully figured and described by Leitgeb.† In this species he finds that the lateral segments cut off from the

* Leitgeb, *l. c.* **2**: 30–33. *pl. 4. f. 7–9.*

† *L. c.* **2**: 10, 11, 13. *pl. 4.*

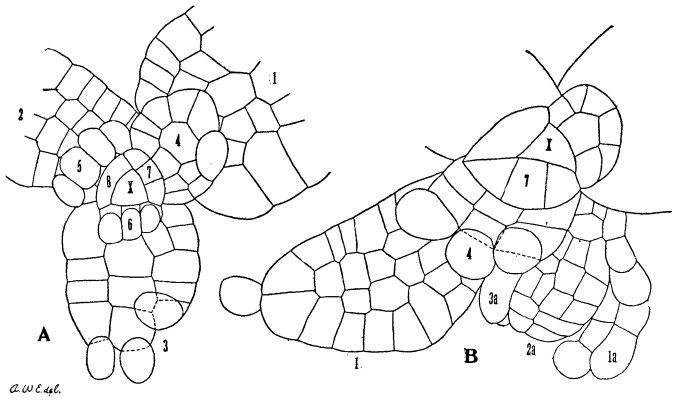
apical cell divide in the usual way into one internal and two external cells. One of these two cells, however, and, apparently, in most cases, the postical one, grows wider than the other and redivides, so that the segment shows three external cells side by side. These three cells correspond with the three teeth at the apex of the mature leaf. In the Hawaiian plant, three external cells are likewise formed in the lateral segments (Fig. A, segment 7), but the mature leaf is subacute and undivided, the three cells, therefore, not giving rise to distinct teeth. This difference is probably not very significant as several species of *Bazzania* with undivided leaves have been described. In each postical segment of *B. trilobata*, one internal and two external cells are formed in the same way as in the lateral segments, but here each of the superficial cells grows wider and divides into two, and the segment shows, therefore, four cells side by side. Each of these cells gives rise to a primordial papilla,* and these four papillae are pushed out by the developing underleaves. The process is, however, irregular, and the lobes of the underleaves often grow out beyond the papillae, leaving them at some little distance from the apex. In each postical segment of the new genus, only three external cells are formed, just as in the lateral segments (Fig. A, segment 6). Each gives rise to a papilla and the three papillae are carried up side by side on the apex of the developing underleaf, which remains broad and undivided (Fig. A, segment 3; Fig. B, segment 4). These three primordial papillae enable us to distinguish at a glance a young underleaf from a young side-leaf, and traces of them may often be detected even in a mature underleaf.

The branching from the lateral segments is the same in both genera and has been briefly described above. It may be remarked, however, that in a branch of this sort, the leaves always maintain a definite sequence; the first leaf is always an underleaf, the second leaf is a side-leaf on the side of the branch turned toward the main axis, and the third leaf is a side-leaf on the side of the branch turned away from the axis. The third leaf, therefore, bears the same relation to the branch that the narrow leaf does to the axis.

In my study of the new genus, I have been unable to find the

* Leitgeb, *l. c.* 2: 15.

very youngest stage of a flagelliform branch. An apical region, however, in which such a branch is found in the third postical segment from the apical cell, shows the following conditions (Fig. B): The underleaf developing from the segment (numbered 1), is narrow and bears a single primordial papilla at the apex; the branch already shows the rudiments of three leaves (numbered 1a, 2a, and 3a), the oldest being a side-leaf on the side away from the underleaf, the second a side-leaf on the side toward the underleaf and the third an underleaf, distinguishable by its three papillae



A. Normal apical region, × 235. *X* Apical cell. 1, 2, 3, etc. Segments in order of age, 3 and 6 showing the young underleaves, each tipped with three primordial papillae.

B. Apical region with young branch in third postical segment from apical cell, × 235. *X*. Apical cell of main axis. 1, 4, 7. Postical segments in order of age; the lateral segments are not numbered as some of the young side-leaves have been dissected away; 1 shows an underleaf with a single primordial papilla, at the side of the young branch. 1*a*, 2*a*, 3*a*. Segments of branch, 3*a* showing the first underleaf, with only two of its three primordial papillae visible.

(only two of which show in the drawing). In this case, therefore, as in the terminal branching from a lateral segment, the third leaf bears the same relation to the flagellum that the underleaf, beside which this specialized branch arises, does to the main axis, and the first two side-leaves are in a corresponding sequence. The same sequence can often be distinguished in an older flagellum (as in Fig. 4, where the second side-leaf is largely concealed), but in some cases the first few leaves are so crowded that it is difficult to make out their true sequence. From the preparation just

described, it is clear, therefore, that the postical segment which is to give rise to a flagellum first divides in the usual way into one internal and two external cells, but that the external cell which normally broadens out and redivides, here develops at once into a branch, leaving only one cell to give rise to the primordial papilla and underleaf. It should be noted also that the flagellum sometimes occurs on the right side of the underleaf and sometimes on the left side, and that both conditions are occasionally found on the same stem.

The peculiar branching just described is of particular interest because it shows that the terminal branching of Leitgeb is not restricted to the postical half of a lateral segment, as that author supposed, but may also occur in either half of a postical segment. The fact that these branches are always specialized as flagella is undoubtedly due largely to their place of origin, and does not affect the point in question. It is, of course, possible that this same type of branching may yet be detected in other genera of the leafy Hepaticae.

The cells of the Hawaiian plant, as is the case with so many alpine and arctic species, are interesting for their extremely thick walls. The thickening is particularly well seen in the cuticle of the leaves. On both surfaces these are densely covered with verruculae which are very distinct on young leaves but become more or less obliterated with age. The trigones of the leaf-cells (Fig. 5) are also conspicuous and project out into the cell-cavities, which are usually distinctly stellate. The trigones are sometimes circular or oval in outline and sometimes tri- or quadri-lobed. Between the trigones the walls are less thickened and sometimes remain very thin, apparently functioning as pits. Along the edges of the leaves (Fig. 6) the cell-walls are irregularly thickened, and it is usually difficult to make out the boundary of the cell-cavity. In the cells of the axis the thickening is also very pronounced (Fig. 7). The superficial cells are here isodiametric, but the internal cells are several times as long as broad. Except for the strongly developed cuticle the thickening is irregular and the cells are provided with pits, which occur in both transverse and longitudinal walls.

The essential characters of Austin's species, both generic and specific, are given in the following description:

Acromastigum gen. nov.

Plants medium-sized, scattered among other hepatics, yellowish-green, becoming brownish with age: stems stiff and wiry, mostly ascending or erect, sparingly branched: vegetative branches of three kinds:—terminal branches from the lateral segments, terminal branches from the postical segments (flagella), intercalary branches axillary to the underleaves (very unusual): rhizoids not abundant: leaves distant or subimbricated, transversely inserted, undivided: underleaves a little smaller than the leaves, undivided: leaf-cells with thickened walls: sexual branches intercalary, arising singly in the axils of the underleaves: ♀ branch very short, its leaves re, duced to the three to five rows of bracts; perianth long and slender. hypogonianthous, the three keels distinct except at the cylindrical base, separated by grooves; unfertilized archegonia borne at the base of calyptra; ♂ spike oblong; bracts in several pairs, strongly concave; antheridia occurring singly; paraphyses wanting; bracteoles similar to the underleaves but smaller: sporophyte not seen. (Name from *ακρον*, summit, and *μαστίξ*, a whip or lash, alluding to the flagella and their place of origin.)

Acromastigum integrifolium (Aust.)

Mastigobryum? integrifolium Aust. Bot. Gazette, **1**: 32. 1875

Bazzania? integrifolia Evans, Trans. Conn. Acad. **8**: 225. 1892.

Dioicous: general characters of stems and branches given above: rhizoids whitish, simple or irregularly branched at the ends, very scanty on ordinary vegetative axes and occurring singly or in small clusters at the bases of some of the underleaves, more abundant on the flagella and less definite in position: leaves spreading widely from the stem, usually curved upward in the outer parts, ovate from a broad base, obtuse or more commonly acute, entire or nearly so, rarely with an indistinct angular tooth near apex: underleaves strongly squarrose, ovate or oblong, truncate or rounded at apex, entire or nearly so: leaf-cells with a very thick verruculose cuticle and conspicuous often confluent trigones but no intermediate thickenings: cell-cavities stellate: ♀ bracts very small and similar to ordinary leaves at base of branch but becoming rapidly larger toward perianth: innermost bracts broadly ovate, gradually narrowed from near the base, shortly dentate or laciniate at apex (usually less than one fourth the length) with slender teeth, otherwise entire or nearly so; innermost bracteole similar; perianth linear-fusiform, composed of a single layer of cells except at the very base, cells more uniformly

thickened than the leaf-cells, mouth of perianth contracted, laciniate, the laciniae long and slender, straight or irregularly curved and distorted, sometimes denticulate, composed of a single row of cells above and usually of two or more toward the base: ♂ bracts in about six pairs, strongly concave, ovate, shortly bi- or tri-denticulate at the apex, the teeth one to three cells long, otherwise entire or nearly so; bracteoles similar to ordinary underleaves but smaller.

Stems 3–8 cm. long, 0.25 mm. in diameter; leaves 0.7 × 0.4 mm.; underleaves 0.5 × 0.3 mm.; leaf-cells at edge of leaf 14 μ in diameter, in the middle 18 μ, and at the base 28 × 23 μ; innermost ♀ bracts 1.7 × 1 mm. (on robust specimens with perianths), perianth 4 × 0.85 mm.; ♂ bracts 0.45 × 0.25 mm., bracteoles 0.35 × 0.15 mm., antheridia 0.15 mm. in diameter.

Mixed with other hepatics. West Maui (Baldwin, 1875); Konahuanui, Oahu (Cooke, 1899). Type specimen in Herb. W. H. Pearson.

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Explanation of Plate 1

1. Plant with perianth, natural size.
2. Part of plant with perianth, × 16.
3. Part of sterile plant, showing ordinary vegetative branching, antical view, × 32.
4. Part of sterile stem, showing base of flagellum, postical view, × 32.
5. Cells from middle of leaf, × 255.
6. Cells from apex of leaf, × 255.
7. Cells from stem in longitudinal section, × 255.
8. Innermost ♀ bracts, × 32.
9. Corresponding bracteole, × 32.
10. Laciniae from mouth of perianth, × 32.
11. Transverse section of perianth, × 32.
12, 13. ♂ bracts, × 32.
14. ♂ bracteole, × 32.